territorial instability is that although both males and females are reproductively active throughout the year, breeding is concentrated during the wet season (Donnelly 1989). If males maintain territories to defend reproductive resources but not food resources (Donnelly 1983), territories might only function to increase male reproductive success by attracting females. During the dry season, when breeding activity is reduced, there may be less incentive for males to maintain territories.

Territory replacement may be a function of territory availability. If the importance of male territoriality decreases in the dry season, the abundance of available territories may not be limiting and replacement may occur less frequently. The time limitations of our study could also be a factor in the low incidence of territorial replacement. More than one day may be required for males without territories to encounter uninhabited territories and establish residence. In addition, more time may be required for neighboring male territory holders to assess the quality and availability of the vacated territory.

The single replacement occurred in a plot with a high density of territorial males. In areas of high male density, encounter rates of uninhabited territories may be higher than in areas of low density. Regions of high male density might also indicate a greater abundance of desirable resources. If so, the incidence of replacement may be higher in regions of high male density.

The absence of any trend in neighboring male territory expansion following removal may also be a result of decreased breeding activity in the dry season. The increased costs of defending a larger territory might not be offset by increased breeding success.

Future studies should investigate potential changes in male *D. pumilio* territorial behavior between wet and dry seasons. Decreased territorial behavior during the dry season may lend support to the hypothesis that the level of reproductive activity influences territoriality of *D. pumilio* males.

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THE MACRO- AND MICRO-DISTRIBUTION OF *TENGELLA RADIATA* (ARANEAE: TENGELLIDAE) AT LA SELVA BIOLOGICAL STATION

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Abstract. *Tengella radiata* is one of the most common spider species in the forest understory at La Selva Biological Station, and yet little is known about its distribution and life history. We examined web distribution in primary and secondary forest and found more *T. radiata* webs in primary forest. Within the primary forest, the distribution of the webs was clumped. It appears that both macrohabitat characteristics of a primary forest (e.g.., abundance of decaying wood) and microhabitat characteristics (e.g..,resource availability) affect the distribution of *T. radiata* webs.

INTRODUCTION

The hammock spider, *Tengella radiata* is a nocturnal species, which builds horizontal webs in buttresses of trees and stilt roots (Mora 1984). Each spider constructs a tunnel adjacent to the main trunk of the tree, in which it resides during the day and when not actively hunting. Webs vary in size, which may be related to the size of the resident spider and its tunnel.

T. radiata belongs to a monogeneric family and is unknown outside of Costa Rica (Santana 1990). Information concerning its range is conflicting. According to Santana (1990), it is found in habitats which vary from "virgin" forest to coffee fields, while Fraser (1992) states that it is found only under closed forest canopies.

We investigated the distribution of *T. radiata* on both a macro- and micro-scale. Since primary forests usually contain larger, more mature trees than secondary forest, we expected more large buttressed trees in primary forest. Because the spider webs are often located in buttresses, we hypothesized that *T. radiata* would be found in greater numbers in primary forest. On a microhabitat scale, we hypothesized that within a tree containing three or more webs, larger webs would be at lower heights than smaller webs. This was based on casual observations of spiders in large buttress trees where larger webs appeared to be located toward the base of the tree and smaller webs at greater heights. In addition, *T. radiata* may catch falling insects in its web, and webs located directly beneath other webs might have to be larger so as not to be completely blocked by those above. Lastly, also based on casual observations, we tested whether *T. radiata* distribution was clumped both within the primary forest as a whole and among trees that contained webs.

METHODS

We conducted our study on 13 and 14 February 1995 at La Selva Biological Station in Costa Rica. On 13 February, we examined macro-distribution of *T. radiata* webs along transects located in primary and secondary forest areas. In the primary forest, we sampled twenty 50 m transects along the Sendero Cantarrana, the Camino Experimental Sur, and the Sendero Oriental. In the secondary forest, we sampled twenty 50 m transects located on the Sendero Sura and the Sendero Tres Rios. Along each transect in both forest types, we recorded all webs that could be visually located within 2 m from the cleared edge of the main trail, on the right side only. For each web we recorded the transect number, substrate, height, and a general description including an estimate of size and any other notable characteristics such as presence of spider and amounts of insects and debris in the web. Lastly, we recorded the number of buttressed trees along each transect, and whether or not webs were present in them.

On 14 February we examined the micro-distribution of *T. radiata* within four trees in primary forest located on the Camino

Circular Lejano and the Camino Circular Cercano. Using the first four trees we encountered with ≥ three webs in them, we recorded for each inhabited web, the dimensions of the major and minor axes, the height above ground, and the diameter of the tunnel. We also made representative maps of the distribution of webs within each tree.

RESULTS

There were significantly more webs in primary (x=1.5/50 m, SD=2.26) than in secondary (x=0.1/50 m, SD=0.45) forest (t=2.718, df=38, P=0.01). There were 31 trees with buttresses in our primary forest transects, seven of which contained spiders, and 30 buttressed trees in our secondary forest transects, two of which contained spiders. Webs were distributed within several microhabitats, with nearly half being in tree buttresses (Table 1).

Table 1. Microhabitat web distribution

Web location	Number
buttress	14
btwn. trunk and vegetation	7
rotting wood	4
walking palm root	7
TOTAL	32

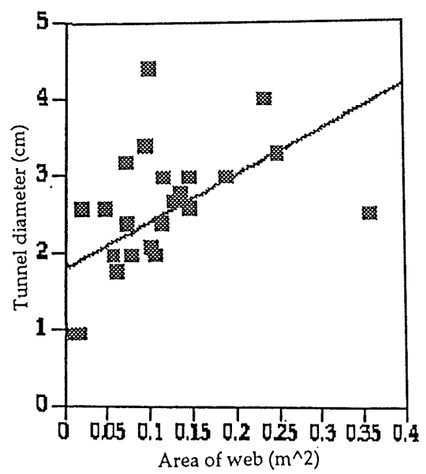

FIG. 1. Correlation of *T. radiata* web area to tunnel diameter (n=26)

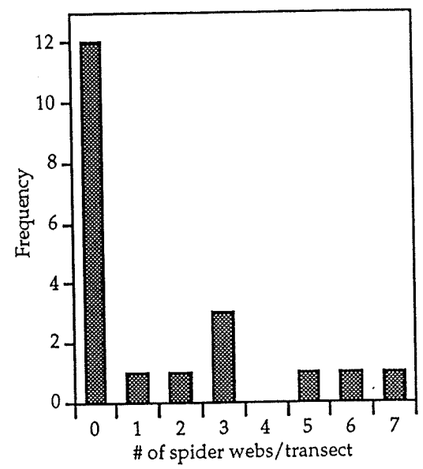

FIG. 2. Frequency distribution of spider webs per transect in primary forest.

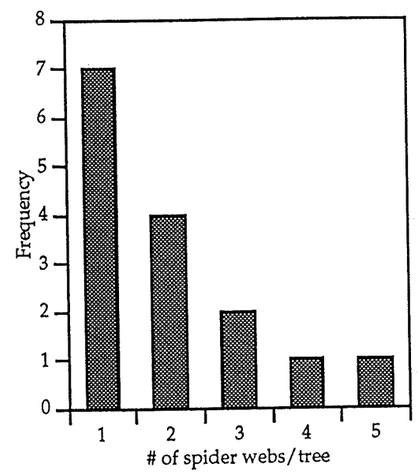

FIG. 3. Frequency distribution of spider webs per tree in primary forest.

Within trees containing webs, there was no significant association between height of web on the tree and area of the web (R^2=0, P=0.9). There was a significant positive correlation, however, between web area and diameter of the tunnel entrance (r=0.55, P=0.004, df=1,24, Fig. 1).

We used an index of dispersion formula to determine the distribution of webs. In the primary forest, the webs were clumped within transects (I=4.3). Many transects contained no webs and a few contained several webs (Fig. 2). However, the webs were evenly distributed within the trees that contain webs (I=0.78). Trees that contained webs had similar numbers of webs (Fig. 3).

DISCUSSION

Our hypothesis that there would be more webs in primary than in secondary forest was supported. This does not, however, appear to be due to a higher abundance of buttresses in primary forest. Our primary and secondary forest transects had similar numbers of buttressed trees, and only a small fraction of these trees contained webs. In addition, many webs in primary forest were in walking palm roots and rotting logs. Therefore, the spiders appear to prefer some aspect of primary forest such as decaying wood, rather than buttresses per se. Finally, since area of web was positively correlated with tunnel diameter, and since tunnel diameter may be indicative of spider size, it appears that large spiders build large webs.

We had expected that webs located towards the bottom of a tree trunk would be larger than those above it, but this was not supported by the data. Web sizes were quite variable at different heights on the tree. It appeared that some webs were not directly above one another, eliminating the need for lower webs to be larger in order to catch falling insects not entering the smaller, higher webs (Fig. 4). Alternatively, the webs may not be intended to capture falling insects, but instead, insects that jump onto their webs from neighboring vegetation. The only insect we observed in a web was a small grasshopper, suggesting falling insects are not the only prey of *T. radiata*. Further study should examine what prey are commonly caught by these webs.

In accordance with our observations, we found webs to be clumped within the primary forest as a whole. This may be due to microhabitat variation within the primary forest that we did not measure, but that are important factors for spider distribution. The spiders were evenly distributed within trees that contained webs, not supporting our initial observations. Territorial behavior often leads to even distributions. However, we do not believe *T. radiata* is territorial since we often found several webs grouped together within a tree. Further study might test if spiders within one tree are genetically related to each other.

It appears that some macrohabitat characteristics of primary forest are more suitable for *T. radiata* webs. In addition, the clumped distribution of webs within the primary forest suggests that there are microhabitat variations affecting the distribution of webs. Further study should try to discover what characteristics of the macro- and microhabitats are most important for the spiders, perhaps focusing on predation risks, interspecific competition, resource availability and abiotic factors.

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FIG. 4. Schematic representation of *T. radiata* webs in *Pentaclethra macroloba*